Trophic relationships in Great Bear Lake using the Ecopath model: Preliminary Analysis

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by

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TABLE OF CONTENTS

TABLE OF CONTENTS	iii
LIST OF TABLES	vi
LIST OF FIGURES	vi
ABSTRACT	v
RÉSUMÉ	vi
1-INTRODUCTION	1
2-SITE DESCRIPTION	1
3-MODELLING FRAMEWORK	3
4- MODEL PARAMETERIZATION	3
4.1-Functional Groups	3
4.2- Model Input Parameters	4
4.2.1- Fish	4
4.2.2- Zoobenthos	5
4.2.3- Zooplankton	5
4.2.4- Primary Production	6
4.3- Balancing the Model	6
4.4- Network Flow Indices, Metrics and Attributes	6
5-TROPHIC NETWORK ANALYSIS	7
5.1- Biomasses, Trophic Flows and Efficiencies	7
5.2-Mixed Trophic Impact and Keystoneness	8
5.3- Fisheries Sustainability	8
5.4- Ecosystem Indices and Attributes	9
6- CONCLUSION AND FUTURE WORK	10
7-REFERENCES	11

LIST OF TABLES

Table1.	List of functional groups and data source for Great Bear Lake Ecopath model.	17
Table 2.	Basic Ecopath parameters (after mass-balancing) used for analysis of Great Bear Lake trophic interactions.	19
Table 3.	Diet composition matrix of GBL Ecopath model showing dietary input value.	19
Table 4.	Transfer efficiencies of flows originating from primary producers and detritus at different trophic levels of GBL ecosystem.	20
Table 5.	System statistics summary of the Great Bear Lake Ecopath Model.	20
Table 6.	Percentage of ascendancy, overhead and capacity on import, internal flow, export and respiration Of the Great Bear Lake model.	21
Table 7.	Primary production required to sustain catches of exploited groups in the Great Bear Lake ecosystem.	21
Table 8.	The comparison of ecosystem indices of some Canadian great lakes.	21

LIST OF FIGURES

Figure 1.	Map of Great Bear Lake showing the management areas.	22
Figure 2.	Flow Diagram of foodweb of Great Bear Lake showing relative biomass and flows between functional groups at various trophic levels.	23
Figure 3.	Simplified trophic models for Great Bear Lake, showing discrete Trophic Levels.	23
Figure 4.	Mixed trophic impact analysis of Great Bear Lake ecosystem.	24
Figure 5.	Keystoneness of different functional groups in Great Bear Lake.	24

ABSTRACT

Janjua, M.Y., Tallman R.F. and Howland K.L. 2015. Preliminary analysis of trophic relationships in Great Bear Lake using Ecopath model. Can. Tec. Rep. Fish. Aquat. Sci. 3137: vi + 24 p.

We used the Ecopath with Ecosim (EwE) ecosystem modelling program to develop a preliminary trophic model for Great Bear Lake (GBL), a relatively pristine ecosystem, to evaluate the utility of this approach in an Arctic/sub-Arctic ecosystem. Model is composed of thirteen functional groups including seven fish groups and four invertebrates groups. The present report documents the model construction, data sources, ranges of data utilised, assumptions, preliminary results, and limitations of the model. The results of trophic network analysis highlighted the importance of the detritus food chain showing 39% of the flows in the lake ecosystem originated from detritus. The mean trophic transfer efficiencies of flows originating from detritus and primary production were 4.9% and 9.1% respectively with an overall mean transfer efficiency of 8.1%. Lake trout were found to be the main keystone species in the ecosystem having relative higher impact. In GBL, primary production was very low and it was a system with low fishing pressure. Therefore a smaller amount of primary production was required and the trophic level of fish catch was within the sustainable range. The higher per-unit ecological cost for lake trout and whitefish as compared to Great Slave Lake showed why a commercial fishery was not feasible for GBL. Comparative analysis of most of the ecosystem indices suggested that the GBL ecosystem was in a mature, stable and healthy state. The relative ascendancy value of GBL was 33%, which was comparatively lower than several other Canadian great lakes indicating better maturity and stability of this pristine ecosystem. The overheads on internal flows also showed that the GBL ecosystem possesses significant reserves to overcome any substantial external disturbances and is stable among comparable ecosystems. Despite being preliminary, this model gives a cohesive view of the ecosystem to explore questions about the functioning of this pristine ecosystem.

RÉSUMÉ

Janjua, M.Y., Tallman, R.F. et Howland, K.L. 2015. Preliminary analysis of trophic relationships in Great Bear Lake using Ecopath model. Rapp. tech. can. sci. halieut. aquat. 3137: vi + 24 p.

Nous avons utilisé le programme de modélisation de l'écosystème Ecopath et Ecosim afin de mettre au point un modèle préliminaire du niveau trophique pour le Grand lac de l'Ours, un écosystème relativement vierge, pour évaluer l'utilité de cette approche dans un écosystème arctique/subarctique. Le modèle est composé de treize groupes fonctionnels, dont sept groupes de poissons et quatre groupes d'invertébrés. Le présent rapport documente la construction du modèle, les sources des données, les aires de répartition des données utilisées, les hypothèses, les résultats préliminaires et les limites du modèle. Les résultats de l'analyse du réseau trophique soulignent l'importance de la chaîne alimentaire de détritus en montrant que 39 % des débits dans l'écosystème du lac proviennent de détritus. L'efficience moyenne du transfert trophique des débits provenant de détritus et de la production primaire a été de 4,9 % et de 9,1 % respectivement, avec une moyenne globale d'efficience du transfert de 8,1 %. Le touladi était la principale espèce clé dans l'écosystème, car elle montrait une incidence relativement plus élevée. Dans le Grand lac de l'Ours, la production primaire était très faible, et il s'agissait d'un réseau faisant l'objet d'une très faible pression de la pêche. En conséquence, une plus faible production primaire était nécessaire et le niveau trophique des prises de poisson se situait à l'intérieur de la fourchette de durabilité. Le coût écologique par unité pour le touladi et le corégone est plus élevé comparativement au Grand lac des Esclaves, ce qui explique pourquoi la pêche commerciale est impossible dans le Grand lac de l'Ours. Une analyse comparative de la plupart des indices écosystémiques laisse entendre que l'état de l'écosystème du Grand lac de l'Ouest est mature, stable et sain. La valeur relative ascendante du Grand lac de l'Ours était de 33 %, ce qui est relativement plus faible que plusieurs autres grands lacs canadiens, et donne une meilleure idée de la stabilité et de la maturité de cet écosystème vierge. L'accent mis sur le débit interne a également démontré que l'écosystème du Grand lac de l'Ours peut compter sur de grandes réserves lui permettant de surmonter toute importante perturbation d'origine externe, et qu'il est stable par rapport à d'autres écosystèmes comparables. Même s'il est préliminaire, ce modèle donne un aperçu cohérent qui permet d'explorer divers aspects du fonctionnement de cet écosystème vierge.

1- INTRODUCTION

Knowledge of species interrelationships within an ecosystem and understanding of ecosystem structure and linkages that govern the system processes is a prerequisite for proper sustainable ecosystem management. Trophic network analysis is becoming a standard tool for ecosystem based fisheries management providing managers with an ability to evaluate the entire food web rather than a single component of the ecosystem (Dame and Christian 2006). Accurate quantitative analysis of trophic interactions can be helpful in answering many important questions in ecology including dynamics of food webs, exploitation and management of resources, and assessment of anthropogenic impacts on ecosystems (Gorokhova and Lehtiniemi 2007). Trophic network analyses estimate the components within a food web using trophic and cycle analyses to evaluate the ecosystem properties. Trophic network analysis can also be used to quantify ecosystem health, integrity and maturity (Christensen and Pauly 1998), and evaluate the magnitude of stress imposed on an ecosystem (Mageau et al. 1998). Knowledge about the ecosystem stability, maturity and health provides us with better information about a system's capabilities allowing for better management.

Ecological models e.g, Ecopath with Ecosim EwE, can be very effective at integrating complex trophic interactions among components of ecosystems (Christensen et al. 2008). There is a long history of using an ecosystem approach in Laurentian Great Lakes management. For example trophic network models have been developed for Lake Ontario (Halfon and Schito 1993; Millard et al. 2001; Stewart and Sprules 2011), Lake Michigan (Krause and Mason 2001), Lake Superior (Kitchell et al. 2000), Lake Erie (Zhu and Johnson 2006) and Lake Huron (Langseth et al. 2010). However, trophic network modelling has not been done for Canadian Arctic and sub-Arctic large freshwater ecosystems. Trophic network modeling of sub-Arctic lakes can be useful in answering questions related to the management of these ecosystems, as has been done in tropical and temperate ecosystems.

A biological system can be considered healthy when it is in a stable condition (Karr et al. 1986). Smol (1992) defined a healthy ecosystem as one that existed prior to any anthropogenic impact. Therefore, generally pristine ecosystems are considered as healthy and stable ecosystems (Karr 1993; Westra 1994). Great Bear Lake (GBL) in the Northwest Territories (NT) Canada, provides a potentially interesting system to study trophic dynamics because of its Arctic location and relatively simple and pristine ecosystem with few anthropogenic impacts. It is among the last remaining pristine great lakes of the world (Evans 2000). It represents one of the only remaining large lake trout populations in North America, thus providing a unique opportunity to study the natural variability of this species in a large lake system (Howland et al. 2007). However, aquatic resources in GBL could be affected by increasing local activities, expanding fisheries and climate change. Global warming and environmental change may be a risk to the GBL ecosystem, which could change the thermal profile of the lake and reduce the duration of winter ice cover on the lake thereby not only affecting lake productivity but the life history patterns and habitat usage of aquatic organisms (MacDonald et al. 2004; Muir et al. 2012). Such changes can be simulated by studying shifts in the structure, function, health and maturity of an ecosystem under various climate change and fishing scenarios with the help of trophodynamic modelling.

Although, relative to other Canadian great lakes, less data are available for the GBL ecosystem components, especially on the biomass estimates of various functional groups. Construction of a preliminary model would be helpful in identifying these data gaps and determining

future research directions. Most of the ecological studies on GBL were conducted around the 1970s and early 1980s. Since 2010, extensive ecosystem level monitoring of the lake ecosystem has been initated. The objectives of this study are to build a trophic network model of the pristine GBL ecosystem during 1970's and create a bench mark for further work on the use of an ecosystem based management approach in this system.

2- SITE DESCRIPTION

Great Bear Lake is located 250 km south of the coast of the Arctic Ocean and intersects the Arctic Circle at the northern extent of the lake (66 °N, 121 °W). Great Bear Lake has five major arms, including Keith, McVicar, McTavish, Dease, and Smith arms (Figure 1). The lake has a surface area of 31,153 km^2 and total volume of 2,236 km^3 (Rao et al. 2012). It is deep (maximum depth 446 m, mean depth 71.7 m), and ultraoligotrophic, remaining mostly isothermal during summer. The lake has a simple food web as it supports 15 fish species (Johnson 1975a,b; Evans 2000; MacDonald et al. 2004). Despite mining on its eastern shores, from 1930's to 1970's it is among the last of the world's large lakes still in a relatively pristine state (GBLWG 2006). Since 2000, the average ice cover duration is 236 days in a year (Howell et al. 2009). Although it is generally un-stratified, well-mixed and temperatures are typically similar from top to bottom , in the more offshore regions, waters remain cold and weakly stratified throughout the summer with temperatures from 4 to 6 °C (Johnson 1975a). Rao et al. (2012) predicted an increase in Great Bear Lake surface temperatures from 0.5 °C to 1 °C except in the northeast corner of lake where a 2 °C increase is projected, possibly resulting in a brief thermal stratification in the deeper waters. Great Bear Lake supports a small scale subsistance fishery for Dene from the community of Deline and also supports a world-class trophy lake trout fishery. The sports fishery has been regulated since 1970 and appears to be sustainable. A commercial fishery was predicted to be unsustainable (Miller 1947) and it is not considered as a management objective (Muir et al. 2012).

Lake trout (*Salvelinus namaycush)*, cisco (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*) are important among fish community in Great Bear Lake(Johnson 1975b). Most of the fish species, with the exception of lake trout and deep-water sculpin, *Myoxocephalus quadricornis*, are confined to the shallow bays. No specific studies have been done on the ecology of cisco in Great Bear Lake, but they appear to be one of the most abundant species in GBL (Falk and Dahlke 1974; Howland pers. comm.). Lake whitefish are mostly confined to bays and generally absent from the open waters. Arctic grayling (*Thymallus arcticus*) are usually found in the mouths of the rivers in lower densities.

Moore (1980) recorded 48 species of phytoplankton, and over 100 species of periphyton from Great Bear Lake. Little information is available on the macrophytes in Great Bear Lake. Johnson (1975b) reported that *Equisetum sp.* occur in few areas of the lake. A total of 20 zooplankton species have been recorded with *Diaptomus sicilis* as the most abundant species (Moore 1981; Johnson 1975b). Zooplankton diversity and abundance appears to decline rapidly in the offshore areas of Great Bear Lake where only five zooplankton species were present (Johnson 1975b). The majority of zoobenthos appears to occur in waters of 20 meters or less, with the amphipod *Pontoporeia* and the mysid *M. relicta* being most abundant, along with chironomids, oligochaetes and sphaerid clams (Johnson1975b). Plankton and zoobenthos standing stocks are generally low in Great Bear Lake (Johnson 1975b) with phytoplankton, attached algae and zooplankton densities among the lowest recorded for freshwater lakes (Moore 1980, 1981). Species composition and standing crop of the

plankton in most of the lake areas due to the similarity in water chemistry and temperature throughout GBL (Johnson 1975a,b; Moore 1980, 1981).

3- MODELING FRAMEWORK

The Great Bear Lake ecosystem was modelled using the trophic modelling software Ecopath with Ecosim, EwE 6.1 (Christensen et al. 2008). Ecopath is an effective modelling tool for analyzing food web structures and trophic interactions by balancing steady state ecosystem models, and has been combined with routines for network analysis based on the approach of Ulanowicz (1986). The basic parameterization of an Ecopath model is based on two 'master' equations (Christensen et al. 2008).

The first equation describes the production term for each functional group:

Production = catch + predation + net migration + biomass accumulation + other mortality

This equation follows the productivity theory developed by Winberg (1956) according to which consumption is the sum of somatic and generative production, metabolic costs and waste products.

The second master equation is based on the principle of conservation of matter within a functional group:

Consumption = production + respiration + unassimilated food

Using network analysis in EwE, the ecosystem network can be mapped into a linear food chain, and energy transfer efficiency can be predicted for various trophic levels. Ecopath also incorporates a number of outputs and holistic indicators that characterize ecosystem properties and act as indicators of ecosystem state, maturity, development and health according to Odum's theory of ecosystem development (Odum 1969). Dynamic routines within Ecopath, e.g. Ecosim, Ecospace and Ecotracer rely on quantified food web structures of the ecosystem and allows exploration of the direct and indirect effects of climate change, fisheries and other anthropogenic activities on the system's biological community and its various components, and can be used for fisheries management purposes.

4- MODEL PARAMETERIZATION

4.1- FUNCTIONAL GROUPS

Johnson (1975b) documented 15 fish species that utilize habitats within GBL during at least a portion of their life history. We used only fish species as functional groups in the modelling which remain in the lake during most of their life cycle and have some important functional role in the ecosystem or in the fisheries (Figure 2). These include lake trout, lake whitefish, lake cisco, Arctic grayling, round whitefish (*Prosopium cylindraceum*) and fourhorn sculpin. Other important forage fish species were combined as "other forage fish" that includes mostly ninespine stickleback (*Pungitius pungitius*) and slimy sculpin (*Cottus cognatus*). Pike (*Esox Lucius*), burbot (*Lota lota*) and longnose sucker (*Catostomus catostomus*) occur infrequently and therefore were not considered as an important part of the GBL ecosystem. Polymorphism in Great Bear lake trout has been established (Blackie et al. 2003; Alfonso 2004, Chavarie et al. 2013). However, in the absence of enough ecological data for the modeling time period, we considered all morphs as a single functional group. For this preliminary model, fish functional groups were not divided into multi-stanza

(multiple life history stage) groups because of data constraints. Among invertebrates, mysids (*Mysis relicta)*, amphipods (*Gammarus lacustris* and *Pontoporeia affinis*) were added as separate functional groups because of their role in foodweb. All other zooplankton were grouped together (mostly *Diaptamus sicilis*) and all other benthic fauna were grouped as benthos (gastropods, insects, chironomids, midges, clams, and oligochaetes). Other important groups included at the 1st trophic level were Primary production (phytoplankton) and detritus. Vadeboncoeur et al (2008) demonstrated that benthic primary production may not be a substantial or negligible component of whole lake primary production in deepest oligotrophic lakes and therefore were not considered for this preliminary model.

4.2- MODEL INPUT PARAMETERS

The basic inputs for an Ecopath model include estimates of biomass (B), biomass turnover rates (production/biomass, P/B), total annual consumption/biomass ratio (Q/B), and ecotrophic efficiency (EE). If one of these parameters is unknown, the Ecopath model can provide estimates using a mass balance routine. Another important input is the diet composition representing trophic interactions among groups; for each predator, the relative proportion of the diet for each type of prey is entered in the input data matrix. The digitalized bathymetry of Great Bear Lake (Long et al. 2007) was used to measure habitat areas for functional groups using Johnson (1975 a) description. Most of the data available and used for the construction of this ecosystem model was from 1970 to 1980, and this Ecopath model represents that time period.

4.2.1- Fish

Biological data from the recreational fishery (creel census) and experimental multi-mesh gill netting on Great Bear Lake during 1984-1985 (Dunn and Roberge 1989) was used to estimate various fish growth parameters using FiSAT (FAO-ICLARM Stock Assessment Tool) and empirical relationships by Froese and Binohlan (2000). For the forage and data deficient species or functional groups, growth data from FishBase (www.fishbase.org) and other literature sources was used. Production/biomass ratio (P/B) is difficult to estimate directly and can be considered equal to the total mortality (Z) (Pauly et al. 2000). For lake trout, total mortality rate calculated by Yaremchuk (1986) based on 1972 to 1985 data, was used. For whitefish, cisco and Arctic grayling, linear catch curve methods were used to calculate total mortality using age-length data and length frequency data by Roberge and Dunn (1988) and Dunn and Roberge (1989) from 1984 to 85 experimental gill net survey.

For unexploited fish groups, natural mortality (M) was estimated using Pauly's empirical relationship (Pauly 1980) and was considered equal to total mortality (Z):

$$M = K^{0.65} * L_{\infty}^{-0.279} * T_c^{0.463}$$

Where, M is natural mortality, K is the curvature parameter of the von Bertalanffy growth function (VBGF), L_{∞} is the asymptotic length (total length in cm), and Tc is the mean water temperature (°C). Consumption/Biomass Ratio (Q/B) was estimated for each fish functional group using the relationship suggested by Palomares and Pauly (1998):

$$\text{Log}\,(Q/B) = 7.964 - 0.204\log W_{inf} - 1.965T + 0.083A + 0.532h + 0.398d$$

Where W_{inf} is the asymptotic weight (g) ; T is an expression for the mean annual temperature of water body, expressed using $T = 1000/K$ ($K = °C + 273.15$) ; A is the aspect ratio ($A = h^2/s$ of the caudal fin of fish, given height (h) and surface area (s)); h is a dummy variable expressing food type

(1 for herbivores and 0 for detritivores and carnivores) and; d is a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores). W_{inf} was calculated from L_{inf} using the length/weight relationship parameters *a* and *b*.

No biomass (B) data were available for fish functional groups in Great Bear Lake. Yaremchuk (1986) had estimated standing stock biomass for lake trout in Great Bear Lake in harvested areas. This biomass was adjusted to the whole lake as per lake trout per habitat area. Lake whitefish biomass was adjusted as per its relative biomass in experimental fish catches (Dunn and Roberge 1989). Biomass of other fish populations was calculated by the Ecopath model by assessing the demands of predators and the amount of fish which can be supported by lower trophic levels, based on food web structure assuming an ecotrophic efficiency (EE) of 0.90 as a standard procedure.

Fish diet matrix was estimated from the published literature. Vander Zanden and Rasmussen (1996) compiled dietary data from over 200 populations of lake trout and its common prey fish species such as coregonids (lake whitefish, round whitefish, cisco), sculpins (slimy and deepwater), and ninespine stickleback . For lake trout and lake whitefish, we used their calculated % volumetric contributions to diet which were based on qualitative diet studies in Great Bear Lake by Miller and Kennedy (1948), Kennedy (1949) and Johnson (1975b). For round whitefish and sculpin, mean dietary data from lakes with similar foodwebs (class 3 lakes in Vander Zanden and Rasmussen1996) were used. For other fish groups a diet matrix was estimated using various publications and reports (Miller 1946; Stewart et al., 2007a, b; Froese and Pauly 2013).

Subsistence and sports fishery at Great Bear Lake were treated as separate fleets. Subsistence harvest has declined in recent decades due to a reduced reliance on dogs. The Great Bear Lake lake trout sport fishery for trophy is world class. The mean subsistence catch and sports catch were estimated using data by Falk et al. (1982), Yaremchuk (1986), Stewart (1996), Muir et al. (2013) and traditional fisheries knowledge gathered during 2012 (unpublished).

4.2.2- Zoobenthos

Johnson (1975b) studied the benthic invertebrate fauna of Great Bear Lake and estimated the density of important groups in different depth zones. The densities of benthic invertebrates differed substantially among the various water depths sampled in Great Bear Lake, with substantial densities of benthic invertebrates occurring only in waters less than 20 m deep. For this study, we calculated the habitat area at different depths using Great Bear Lake bathymetry data digitalized from Canadian Hydrographic Service chart 6390 (Long et al. 2007). Densities of the mysid (*Mysis relicta*) and amphipods (*Pontoporeia affinis, Gammarus lacustris*) at different depths was estimated from Johnson (1975b) and combined with mean individual biomass calculated after Balcer et al. (1984), EPA (2003) and Benke et al. (1999) to approximate the total biomass in the lake. All other benthic invertebrates were grouped together as other benthos and their biomass was estimated by the Ecopath assuming an EE of 0.90. P/B ratios were calculated using the empirical relationship of Brey (1999) for lake benthic invertebrates and taken from literature (Waters 1977). Diets of amphipods and mysids were estimated from Moore (1979) and Kitchell et al. (2000).

4.2.3- Zooplankton

Johnson (1975b) and Moore (1981) described the zooplankton community in GBL comprehensively. The results of these studies suggest that Great Bear Lake has the lowest diversity and density of zooplankton among large lakes in North America, with offshore areas being less

productive compared to nearshore areas. *Diaptomus sicilis* was the most abundant species in all areas of the lake. The data from Johnson (1975b) was used to calculate the individual mean size and total biomass of zooplankton (Balcer et al. 1984; EPA 2003; Benke et al. 1999). The mean P/B ratio was based on literature (Waters 1977; Jorgensen 1977).

4.2.4- Primary Production

Moore (1980) provided information on the structure of phytoplankton communities in Great Bear Lake showing that the standing crop of phytoplankton in the lake was among the lowest found in freshwater systems, ranging from 20 to 91 $mg.m^{-3}$. In absence of any other measurement for standing phytoplankton biomass, we used Moore's data to calculate mean annual standing stock phytoplankton biomass for the whole lake. The annual mean phytoplankton primary production for Great Bear Lake, reported as 4 $gC.m^{-2}.year^{-1}$ (6-252 $mgC.m^{-2}.d^{-1}$) by Schindler (1972) and Duthie (1979), was used to calculate P/B ratio.

Detritus (biogenic endogenous matter of the lake) biomass (D) was calculated using the following empirical relationship:

Log D = 0.954logPP + 0.863logE - 2.41 (Christensen et al. 2005)

Where D= detrital biomass (g/m^2); PP = primary production (in $gCm^{-2}year^{-1}$); E = euphotic depth in meters.

4.3- BALANCING THE MODEL

In Ecopath, the degree of energy 'imbalance' of each functional group is usually determined by examining the ecotrophic efficiency (EE). A value of EE greater than 1 indicates that total demand exceeds total production. An approach was developed to balance the model by making adjustments to functional groups having the EE greater than 1. Adjustments to the diet were made first as diet data have low reliability. If the changes to the diet had only a minimal effect, then changes to B, P/B or Q/B were made. Another balancing check we made was to ensure that all the model parameters complied with physiological and thermodynamic constraints using two other important diagnostic indices. Gross food conversion efficiency (P/Q ratio) usually ranges from 0.1 to 0.3. Thermodynamic constraints limit Production/Respiration (P/R) ratio to a realized range from 0 to 1. For this model, both indices were within the thermodynamic constraints limits.

4.4- NETWORK FLOW INDICES, METRICS AND ATTRIBUTES

Ecological analysis integrated in EwE was used to examine a number of indictors describing trophic flows derived from thermodynamic concepts, information theory, and network analysis. These indices can be used to evaluate the whole ecosystem state in terms of its maturity, efficiency and health. The 'Lindeman spine' analyses developed by Ulanowicz (1995) reduces the complex food webs into a simple chain of trophic interactions and can also be used to calculate transfer efficiencies between trophic levels. Mixed Trophic Impact (MTI) are calculated by multiplication of the matrix of the direct impacts compiled by using the matrices of positive direct impact of diet and negative direct impact of consumption (Ulanowicz and Puccia 1990). MTI are indicators of the relative impact of change in the biomass of one functional group on the other functional groups of the ecosystem. Keystoneness (KS) index (Libralato et al. 2006) scales trophic impact with biomass, "penalizing" a stock with high abundance by giving high values to stocks which have large impacts while maintaining a low biomass. Keystone species have a structuring role in their food webs. Various

ecosystem metrics were estimated to characterize and quantify the ecosystem structure of GBL. Several indices of ecosystem maturity, stability and resilience can be been derived from EwE mass-balanced models (Christensen 1995). These ecosystem attributes estimated by Ecopath models and methods of Odum (1969), Ulanowicz (1986), Christensen (1995) and Xu et al. (2001) were used to assess maturity, stability and health of GBL compared to the other lakes such as GSL, still healthy but altered Lake Superior ecosystem model (Kitchell et al., 2000) and transitioning Lake Ontario ecosystem model (Halfon and Schito,1993). These Laurentian great lakes models were representing almost the same time period.

5- TROPHIC NETWORK ANALYSIS

A balanced model was constructed for the Great Bear Lake ecosystem. The input parameters and basic estimates of the Ecopath model are given in Tables 2 and 3. A pedigree index of 0.40 was estimated for the Great Bear Lake Ecopath model which conformed to the middle level of overall acceptable quality (Morissette et al. 2006).

5.1- BIOMASSES, TROPHIC FLOWS AND EFFICIENCIES

The average fish biomass density obtained from the model was 0.89 $t.km^{-2}$, which was within the limits that could be supported by the primary production as per descriptions of Downing et al. (1990). Lake trout was dominant in GBL followed by cisco in regards to fish biomass in the lake. Ecopath models estimated potential biomass of cisco and deepwater sculpin as 26% and 20% respectively, of the total fish biomass in GBL by assessing the demands of predators and the amount of fish which can be supported by lower trophic levels. These results might appears to be somewhat overestimated if compared with experimental catches. However, Johnson (1975b) found lake cisco occurred more frequently in the diet of lake trout than was expected from net samples in GBL. Because of adaptation to extreme oligotrophy, *Myoxocephalus quadricornis* are able to utilize all regions of the lake in GBL (Johnson 1975) therefore its overall biomass density is comparatively high in the ecosystem.

As expected, Ecotrophic efficiency values were low for apex predator lake trout. It was high for primary production and indicative that a large proportion of primary production was utilized in the ecosystem which is typical for ultra-oligotrophic lakes. In the absence of biomass estimates, EE of most of the functional groups were used as 0.95 in the model. Ecopath measured the average trophic level at which the group received energy and calculated the fractional trophic level (TL) for each functional group. The highest realized trophic level was 3.9 for the lake trout, which is a slightly lower when compared to other lakes similar lakes (Vander Zanden and Rasmussen 1996, Kitchell et al. 2000). This could be a result of ecological morphtypes consuming different prey items. A specifically piscivore type may have a bit higher trophic position in the ecosystem. Lake whitefish, the other important fish group, was at trophic level 3.14. Ecopath's network analysis summarized the food web into a "Lindeman spine", allowing for the calculation of energy flows between different trophic levels and transfer efficiencies. Primary production in the lake was estimated to be approximately 40.18 t $km^{-2}year^{-1}$. 43.84 t $km^{-2}year^{-1}$ of detritus were cycled through the lake (Fig. 3). In the GBL ecosystem, 39.61 t $km^{-2}year^{-1}$ detritus was formed annually of which 15.79 t $km^{-2}year^{-1}$was consumed. The trophic flow from TL I to TL II was 44.41 t $km^{-2}year^{-1}$, from TL II to TL III was 2.74 t $km^{-2}year^{-1}$ and from TL III to TLIV was 0.402 t $km^{-2}year^{-1}$ only (Fig 3).. The transfer efficiencies with these flows were, 6.2%, 14.7%, and 5.8%, respectively. The mean trophic transfer efficiencies originating from detritus and primary production were 4.9% and 9.1, %

respectively with a mean value of 8.1 (Table 3) which was in the range of reported transfer efficiency values in the literature (Libralato et al. 2008). In a more mature and stable ecosystem, primary production should be utilized more effectively. In GBL, transfer efficiency of primary production is almost double when compared to Lake Superior (Kitchell et al. 2000) and Lake Ontario (Halfon and Schito 1993). Comparatively, low trophic transfer efficiencies of Laurentian Great Lakes could put them in a condition of impaired health.

5.2- MIXED TROPHIC IMPACT AND KEYSTONENESS

The mixed trophic impacts (MTI) are indicators of the relative impact of change in the biomass of one functional group on the other functional groups in the ecosystem. The mixed impact is a sum of these direct and indirect impacts. Mixed trophic impacts (MTI) analysis showed competitive interactions among functional groups at the same trophic level. Primary production and detritus had positive impacts on other functional groups (Figure 4). Benthic fauna also have a strong positive impact on fish groups at middle trophic levels. Lake trout had a strong negative impact on all the fish functional groups. Impact of both subsistence and sports fisheries was almost negligible on all the functional groups.

Keystone species are defined as relatively low biomass species with a structuring role in their food webs. Libralato et al. (2006) introduced the keystoneness (KS) index which scales the impact of a group on the whole ecosystem through attributing high values to stocks having large impacts while maintaining a comparatively low biomass. In the GBL ecosystem, lake trout were found to be the main keystone species. It showed a relatively higher impact and therefore could have an important role in maintaining the structure of ecosystem (Figure 5). Keystone species are very important from a climate change prospective. A strong response to climate by keystone species may have dramatic effects on the food web structure (Blenckner 2005), especially in simple food chains like GBL. Lake trout is a keystone predator in many lakes in the lower Mackenzie River basin. Low food supply and temperatures, however, keep lake trout near physiological limits for survival and therefore they are sensitive to changes in either temperature or food supply initiated by climate change (McDonald et al. 1996).

5.3- FISHERIES SUSTAINABILITY

Primary Production Required (PPR) is the energy required to support consumption or catches in the ecosystem. It is an index of the ecosystem efficiency similar to "emergy" concept and has been conceived as an ecological foot print (Pauly and Christensen, 1995). It is an indicator quantifying the fisheries pressure since it can be easily compared and scaled with primary productivity of the system (Pauly and Christensen 1995, Tudela et al. 2005). Primary production required to sustain fisheries % PPR (PPR as a part of total PP), in combination with Trophic Level of Catch (TLc), is a quantitative ecosystem index to assess the effect of fisheries on an ecosystem (Pauly and Christensen 1995, Tudela et al. 2005). The sensitivity of an ecosystem to fisheries depends on both TLc and % PPR. The total primary production required to sustain catches was calculated as 0.72 $t.km^{-2}$, of which lake trout and lake whitefish required 0.62 $t.km^{-2}$ and 0.06 $t.km^{-2}$, respectively (Table 7). The average fish catch in Great Bear Lake during the modeling period required only 1.06 % of the available primary productivity (%PPR). The mean trophic level of fish catch (TLc) was 3.55. In Great Bear Lake, primary production is very low, however, it is also a system with low fishing pressure. TLc and % PPR to sustain fish catch looks well within the sustainable range as per the framework developed by Tudela et al. (2005). Libralato et al. (2008) developed a new index (loss in production index, L Index), to support ecosystem-based management

of fisheries for the evaluation of sustainability of fisheries. L index takes into account ecosystem properties (primary production and transfer efficiency) and features of fishing activities (TLc and PPR). L Index for GBL was 0.0003 showing 100 % probability that it is a sustainably fished ecosystem as per the definition of Libralato et al. (2008). The current harvest of lake trout in Great Bear Lake is below the maximum sustainable yield (Low and Taylor 2002). However, much higher per unit cost for GBL whitefish as compared to Great Slave Lake shows why a commercial fishery is not feasible in Great Bear Lake. Miller (1947) concluded that most of the offshore part of GBL is like a biological desert and not suited for large fisheries and even a small harvest could result in rapid changes in the structure of fish populations. Although lake trout standing crop looks sufficient in Great Bear Lake, the low primary productivity implies that harvest rates must be kept at low levels in order to avoid over-fishing (Johnson,1976, MacDonald et al. 2004).

5.4- ECOSYSTEM INDICES AND ATTRIBUTES

Properties and attributes of the GBL ecosystem are listed in Table 5. Net primary production (PP) provides an index of activity at lower trophic levels while respiration (R) provides a measure of activity at the upper levels. Total system throughput (TST) represents all the energy flows within an ecosystem and shows the size of the entire system in terms of flow. In the GBL ecosystem, consumptions dominate the TST (42%) followed by flow into detritus that were almost 24% of the energy flows. Net system production was comparatively low in Great Bear Lake. Net system production should be large in immature systems and low in mature or developed ones. The connectance index (CI) is a measure of the percentage of realized links over the number of possible links and is a measure of foodweb complexity. The connectance index was estimated at 0.29 which is relatively high among the comparable lake ecosystems. System omnivory index (OI) was 0.09 which is almost at the same level with Great Slave Lake. The low values for omnivory index may also result from systems dependence on detritus as a source of energy. Ecosystems that are less dependent on detritus have higher OI values because the organisms need to diversify their energy sources (Christensen 1995, Vasconcellos et al. 1997).

Ecopath provides important information that can allow us to establish the status of an ecosystem in terms of maturity and stability. Many attributes related to an ecosystem's development and maturity theories (developed by Odum, 1969) have been incorporated in the Ecopath models which are considered as descriptors of ecosystem maturity, stability and health (Christensen 1995). Ecosystem maturity is perceived as a descriptor and indicator of ecosystem health. An undisturbed or pristine ecosystem is to be mature *sensu* Odum (Odum 1969). However, when ecosystems are disturbed, especially by fishing, their maturity is expected to decrease (Christensen 1995). Being a pristine and less disturbed ecosystem with small fishing pressure, the Great Bear Lake ecosystem should be more mature stable and healthy than other lake ecosystems having large fisheries. We compared ecosystem attributes of the Great Bear Lake ecosystem model with few other Canadian great lakes ecosystem models, either having the same number or similar types of functional groups or having similar ecological conditions including Great Slave Lake (Janjua and Tallman 2013), Lake Superior (Kitchell et al. 2000) and Lake Ontario (Halfon and Schito 1993). Comparison of most of the ecosystem indices of Great Bear Lake with other great lakes of North America showed comparative greater stability of the pristine Great Bear Lake (Table 8).

Primary production/respiration (Pp/R) and primary production/biomass (Pp/B) are related to ecosystem maturity as energetic attributes. In the early stages of ecosystem development, primary

production (Pp) is more than respiration, therefore (Pp/R) ratio will be greater than 1. However, with maturity this ratio decreases until respiration and and primary production are equivalent and it reaches close to unity. The ratio between total primary production (PP) and total respiration (R) was 1.44, which is much closer to unity compared to other great lakes. With the system maturity, biomass also accumulates and as a result, the primary production (Pp/B) ratio decreases. The relatively higher values of Pp/B in GBL ecosystem indicate accumulation of biomass over time and system stability. The ratio of total system biomass to total system throughput (B/TST) is directly proportional to the system maturity and should be higher in mature and stable ecosystems (Christensen and Pauly 1998, Christensen and Walters 2004). The B/TST for GBL is almost 20 times higher than Lake Superior and Lake Ontario, showing that comparatively much less energy flow is required to support the biomass in the GBL ecosystem. The degree of recycling in an ecosystem can be measured with Finn's Cycling Index (FCI) (Finn 1976), which expresses the fraction of the total system throughput that is recycled. This index can be used as a measure of system maturity, resilience and stability (Christensen 1995, Vasconcellos et al. 1997). FCI value for the GBL ecosystem is much higher than GSL, Lake Superior and Lake Ontario (Table 7).

The FCI for the GBL was higher in comparison to Great Slave Lake, Lake Superior and Lake Ontario showing its stability in a pristine condition. Mature ecosystems recycle a large amount of throughput compared to developing ecosystems and have higher FCI (Finn 1976; Odum 1969). Christensen (1995) found a strong correlation between the FCI and the ecosystem maturity rankings. Recycling is critical in modulating the ecosystem stability because systems with high capacity to recycle detritus are better equipped to recover from external perturbations (Vasconcellos et al. 1997). Relative ascendancy is another key index characterizing the maturity of an ecosystem (Ulanowicz 1986, Christensen 1995). Ascendency is a measure of the average mutual information in a system, scaled by system throughput, and is derived from information theory (Ulanowicz and Norden 1990). The relative ascendancy (Ascendancy/Capacity) is the fraction of possible organization that is actually realized (Ulanowicz 1986) and is negatively correlated with ecosystem maturity and can be used to evaluate ecosystem health (Christensen 1995; Brando et al. 2004). The relative ascendency value was low at 33 %, with a high overhead of 67 %. The relative ascendancy value of Great Bear Lake is comparatively lower than comparative lakes ecosystems indicating greater maturity and stability (Table 7). The overheads on internal flows (redundancy), also derived from information theory, may be seen as a measure of system stability (Christensen 1995). The high overheads on internal flows (Table 5) show that the GBL ecosystem possesses significant reserves to overcome substantial external disturbances and is stable among comparable ecosystems for this attribute.

6- CONCLUSION AND FUTURE WORK

This is a first attempt to model a sub-Arctic freshwater ecosystem in North America and to better understand the trophic structure and function of the pristine GBL ecosystem. An ecosystem approach to fisheries management in this lake is identified as an important research goal by the Great Bear Lake Working Group (GBLWG 2005, Muir et al. 2012). Trophic network modeling of Great Bear Lake has provided some useful information for the purpose of ecosystem based fisheries management. Despite being preliminary, this model gives a cohesive view to explore questions about the functioning of this pristine ecosystem. It provides a heuristic approach for evaluating interactions of all important components and groups in this simple ecosystem. The Great Bear Lake ecosystem shows the general characteristics of a stable ecosystem. As expected, the pristine GBL looks more mature and developed as compared to commercially fished Great Slave Lake and the Lake Superior

ecosystems, and changing Lake Ontario ecosystem as per definitions of Odum (1969), Ulanowicz (1986) and Christensen (1995). According to traditional beliefs and Dene elders' sayings, Great Bear Lake will be one of the last places where there will be freshwater and good food (GBLWG 2006). According to the sayings of Ayah, a Dene prophet from Déline "my people will be the very last ones to have fish". Our results also confirm a comparative pristine and stable position of GBL ecosystem during the modelling period which supports these beliefs. A traditional knowledge study conducted on the Great Bear Lake ecosystem (unpublished) at Déline during 2012 showed that the fish population and some other ecosystem characteristics has not been changed since the modelling period. Modelling new data in coming years and comparison with results from this model can provide some informative and useful results.

However, there are many limitations to the present study due to data gaps and uncertainties associated with the input parameters. Our present analyses are focused more on the characterization of the basic ecosystem attributes and flows. Further studies to better characterize the key elements of the ecosystem including studies on fish and lower trophic level biomass, and morphotypes of lake trout are going on under the NWT- Cumulative Impact Monitoring Program (CIMP) project which will improve the input data and help in improving the characterization of the ecosystem. Comparison of bioenergetics and network analysis of a model based on fresh data with the present model will be useful to study potential impacts of climate change. At present, it is difficult to use this model for predictive simulations because of a lack of time-series data especially related to biomass and primary productivity. Role of competitive interactions may be underestimated in such types of simulations when data are not available for time series fitting and adjustment of vulnerabilities. Therefore, it is necessary to acquire adequate time-series data to adjust vulnerability. Ongoing multiyear research on the Great Bear Lake ecosystem will be helpful in developing the time series information.

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TABLES

Table1: List of functional groups and data source for Great Bear Lake Ecopath model

Functional Group	Parameter	Data source
Lake trout (*Salvelinus namaycush*)	Life history parameters and habitat	Johnson,1975, Dunn and Roberge 1989; Roberge and Dunn 1988, Yaremchuk 1986
	Biomass	Yaremchuk 1986
	P/B	Yaremchuk 1986
	Q/B	Palomares and Pauly 1998
	Diet	Johnson 1975, Vander Zanden and Rasmussen 1996
	Catch	Steward 1996, TEK (unpublished)
Lake cisco (*Coregonus artedi*)	Life history parameters and habitat	Falk and Dahlke 1974, Dunn and Roberge 1989;
	Biomass	Estimated by Ecopath model
	P/B	Pauly 1980
	Q/B	Palomares and Pauly 1998
	Diet	Vander Zanden and Rasmussen 1996
	Catch	Steward 1996, TEK (unpublished)
Lake whitefish (*Coregonus clupeaformis*)	Life history parameters and habitat	Falk and Dahlke 1974; Dunn and Roberge 1989;
	Biomass	Indirect, Dunn and Roberge 1989
	P/B	Pauly 1980
	Q/B	Palomares and Pauly 1998
	Diet	Johnson 1975, Vander Zanden and Rasmussen 1996
	Catch	Steward 1996, TEK (unpublished)
Arctic grayling (*Thymallus arcticus*)	Life history parameters and habitat	Falk and Dahlke 1974, Dunn and Roberge 1989,
	Biomass	Estimated by Ecopath model
	P/B	Pauly 1980
	Q/B	Palomares and Pauly 1998
	Diet	Steward 2007 a
	Catch	Steward 1996, TEK (unpublished)
Sculpin Deepwater sculpin *(Myoxocephalus thompsonii)*	Life history parameters and habitat	Froese and Pauly 2011
	Biomass	Estimated by Ecopath model
	P/B	Pauly, 1980
	Q/B	Palomares and Pauly 1998
	Diet	Froese and Pauly 2011
Round whitefish (*Prosopium cylindraceum*)	Life history parameters and habitat	Falk and Dahlke 1974, Dunn and Roberge 1989
	Biomass	Estimated by Ecopath model
	P/B	Pauly 1980
	Q/B	Palomares and Pauly 1998
	Diet	Steward 2007 b
Other forage fish ninespine stickleback (*Pungitius pungitius,* Slimy sculpin (*Cottus cognatus*)	Life history parameters and habitat	Froese and Pauly 2011
	Biomass	Estimated by Ecopath model
	P/B	Pauly 1980
	Q/B	Palomares and Pauly 1998
	Diet	Froese and Pauly 2011
Mysis (*Mysis relicta*)	Abundance / Biomass/Habitat	Larkin 1948; Johnson 1975
	P/B	Waters 1977; Jorgensen 1977; Kitchell et

		al. 2000
	Q/B	Estimated by Ecopath model
	Diet	Grossnickle 1982; Kitchell et al. 2000
Zooplankton Mostly *Diaptamus sicilis and Cyclops* sp.	Abundance / Biomass/ Habitat	Johnson 1975, Moore 1981
	P/B	Waters 1977; Jorgensen 1977
	Q/B	Estimated by Ecopath model
	Diet	Kitchell et al. 2000
Amphipods (*Gammarus lacustris and Diporeia affinis*)	Abundance / Biomass/ Habitat	Larkin 1948; Johnson 1975
	P/B	Waters 1977; Jorgensen 1977, Kitchell et al. 2000
	Q/B	Estimated by Ecopath model
	Diet	Moore1977
Other benthos gastropods, chironomids, midges, other insects larvae, clams, oligochaetes	Abundance / Biomass/ Habitat	Estimated by Ecopath model / Johnson 1975
	P/B	Waters 1977, Jorgensen 1977, Kitchell et al. 2000
	Q/B	Estimated by Ecopath model
	Diet	Kitchell et al. 2000
Primary production Mostly phytoplankton	Biomass	Moore, 1980
	Production	Schindler 1972
Detritus non-living particulate organic material	Biomass	Empirical estimation (Christensen et al. 2005)

Table 2. Basic Ecopath parameters (after mass-balancing) used for analysis of Great Bear Lake trophic interactions. P/B and Q/B are annual rates while EE and P/Q are dimensionless. Bold values were calculated by Ecoptah model.

	Group	TL	B $t.km^{-2}$	P/B $year^{-1}$	Q/B $year^{-1}$	EE	P/Q	Catch ($t.km^{-2}.year^{-1}$)		
								Sub.	Sports	Total
1	Lake trout	**3.90**	0.31	0.24	1.30	**0.09**	**0.18**	0.00086	0.00083	0.00169
2	Lake cisco	**3.17**	**0.23**	0.65	2.30	0.95	**0.28**	0.00072	-	0.00072
3	Lake whitefish	**3.14**	0.08	0.35	1.55	**0.55**	**0.23**	0.00060	-	0.00060
4	Arctic grayling	**3.08**	**0.00**	0.70	2.50	0.95	**0.28**	0.00014	0.00005	0.00019
5	Sculpin	**3.09**	**0.18**	0.45	2.90	0.95	**0.16**	-	-	-
6	Round whitefish	**3.00**	**0.00**	0.51	2.20	0.95	**0.23**	-	-	-
7	Other forage fish	**3.09**	**0.09**	0.87	5.10	0.95	**0.17**	-	-	-
8	Mysis	**2.56**	0.28	2.00	**8.00**	**0.40**	0.25	-	-	-
9	Zooplankton	**2.11**	2.16	3.50	**14.00**	**0.63**	0.25	-	-	-
10	Amphipods	**2.00**	1.79	2.00	**8.00**	**0.14**	0.25	-	-	-
11	Other benthos	**2.00**	**0.23**	2.00	**8.00**	0.90	0.25	-	-	-
12	Primary production	**1.00**	3.04	13.22	0.00	**0.71**		-	-	-
13	Detritus	**1.00**	0.50			**0.56**		-	-	-

Table 3. Diet composition matrix of GBL Ecopath model showing dietary input value. Numbers on top are Ecopath functional groups (predators) preying on prey groups (left). Different dietary contributions were adjusted based on a mass balance approach.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11
1	Lake trout	0.01										
2	Lake cisco	0.35										
3	Lake whitefish	0.04										
4	Arctic grayling	0.01										
5	Sculpin	0.19										
6	Round whitefish	0.01										
7	Other forage fish	0.15	0.01	0.12	0.05							
8	Mysis	0.07	0.15	0.01		0.15		0.08				
9	Zooplankton		0.75		0.11	0.06		0.40	0.50	0.10		
10	Amphipods	0.03		0.32	0.28	0.55	0.20	0.30				
11	Other benthos	0.14	0.10	0.55	0.37	0.24	0.80	0.21				
12	Primary production								0.25	0.90	0.05	0.10
13	Detritus								0.25		0.95	0.90
14	Import	0.01			0.20							

Table 4. Transfer efficiencies of flows originating from primary producers and detritus at different trophic levels of GBL ecosystem.

Source / Trophic level	II	III	IV
Primary Producer	6.5	14.6	7.9
Detritus	5.7	14.8	1.4
All flows	6.2	14.7	5.8
Proportion of total flow originating from detritus: 0.39			
Transfer efficiencies (calculated as geometric mean for TL II-IV):			
From primary producers: 9.1%			
From detritus: 4.9%			
Total: 8.1%			

Table 5. System statistics summary of the Great Bear Lake Ecopath Model. Various efficiencies and indices are dimensionless

Parameter	Value	Units
Sum of all consumption	50.62	$t.km^{-2}.y^{-1}$
Sum of all exports	12.26	$t.km^{-2}.y^{-1}$
Sum of all respiratory flows	27.94	$t.km^{-2}.y^{-1}$
Sum of all flows into detritus	28.05	$t.km^{-2}.y^{-1}$
Total system throughput	118.86	$t.km^{-2}.y^{-1}$
Sum of all production	52.74	$t.km^{-2}.y^{-1}$
Calculated total net primary production	40.19	$t.km^{-2}.y^{-1}$
Net system production	12.25	$t.km^{-2}.y^{-1}$
Total biomass (excluding detritus)	8.39	$t.km^{-2}.y^{-1}$
Total catches	0.0032	$t.km^{-2}$
Mean trophic level of the catch	3.55	
Gross efficiency (catch/net p.p.)	0.00008	
Total primary production/total respiration	1.44	
Total primary production/total biomass	4.79	
Total biomass/total throughput	0.07	
Total biomass/total production	0.16	

Table 6. Percentage of ascendancy, overhead and capacity on import, internal flow, export and respiration Of the Great Bear Lake model.

Source	Ascendency (flowbits)	Ascendency (%)	Overhead (flowbits)	Overhead (%)	Capacity (flowbits)
Internal flow	80.3	18.8	201.5	47.3	281.8
Export	25.5	6	14.7	3.5	40.2
Respiration	34.4	8.1	69.5	16.3	103.9
Total	140.3	32.9	285.8	67.1	426.1

Table 7. Primary production required to sustain catches of exploited groups in the Great Bear Lake ecosystem

Group name	TL	PPR	PPR/ catch	PPR/ Tot. PP (%)	PPR/u. catch
Lake trout	3.90	0.62	368.86	0.91	5.41
Cisco	3.17	0.03	36.09	0.04	0.53
Lake whitefish	3.14	0.06	102.69	0.09	1.50
Arctic Grayling	3.08	0.01	52.20	0.01	0.76
Total	3.55	0.72	225.25	1.06	3.30

Table 8. The comparison of ecosystem indices of some Canadian great lakes

	Great Bear[1]	Great Slave[2]	Superior[3]	Ontario[4]
Total system throughput	118.86	600.88	3547.73	25624.81
Total primary production	40.19	252.56	1589.09	11012.05
Total system production	52.74	283.81	1640.74	11180.35
Total primary production/respiration	1.44	3.09	1.60	18.06
Total primary production/biomass	4.79	15.60	127.54	165.34
Biomass/ total system throughput	0.070	0.030	0.004	0.003
Biomass/ total system production	0.16	0.08	0.01	0.01
Connectance Index	0.29	0.25	0.20	0.20
System omnivory index	0.09	0.08	0.09	0.07
Finn's cycling index	10.58	3.33	0.39	3.62
Finn's mean path length	2.96	2.38	2.23	2.24
Relative Ascendency (%)	33.02	38.20	50.4	49.0
Redundancy (Overheads on internal flows)	47.3	46.8	37.9	41.1

1- Present work , Janjua & Tallman 2013 , Halfon E. and Schito 1993,Kitchell et al 2000.

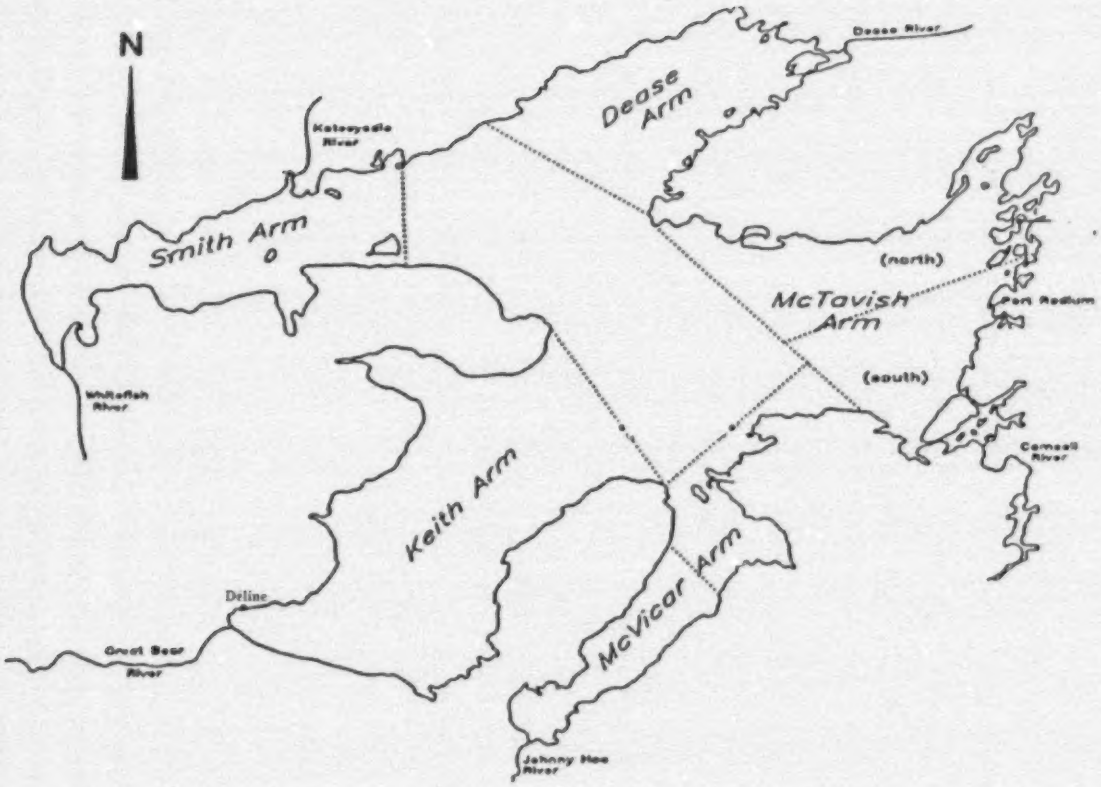


Figure 1. Map of Great Bear Lake showing the management areas

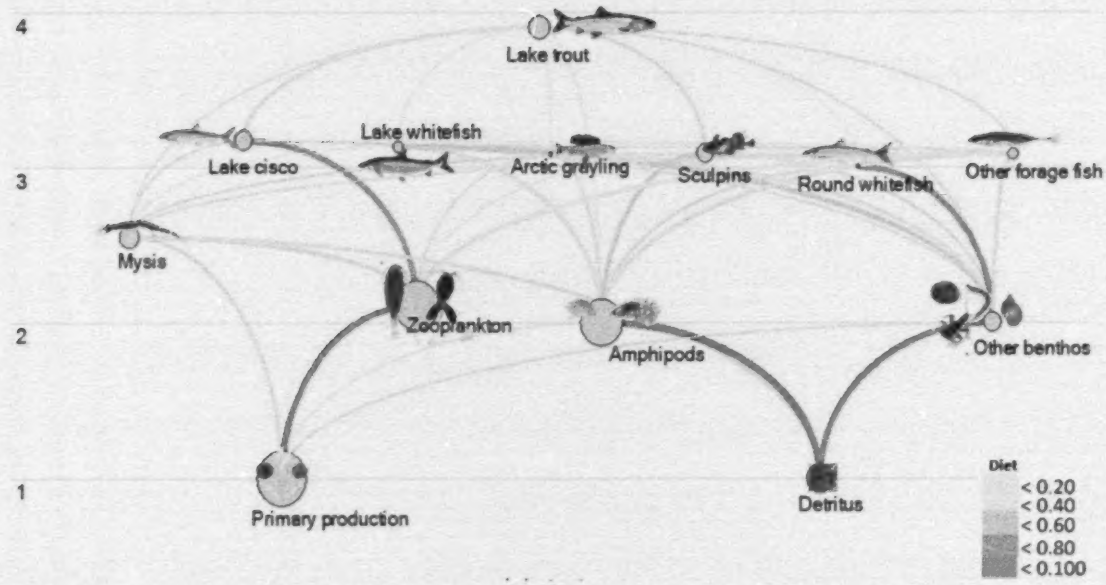
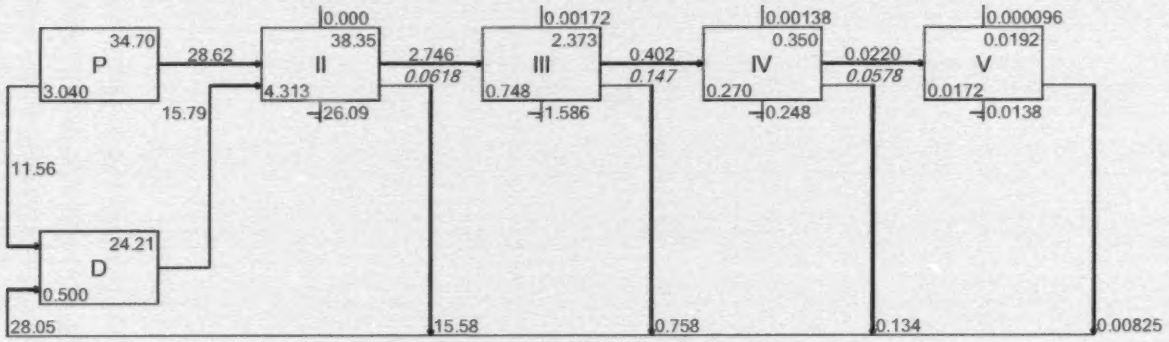


Figure 2. Flow Diagram of foodweb of Great Bear Lake showing relative biomass and flows between functional groups at various trophic levels.



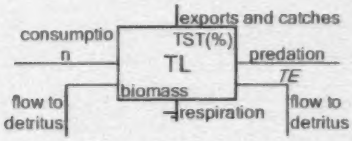


Figure 3. Simplified trophic models for Great Bear Lake, showing discrete Trophic Levels. Horizontal arrows denote flows from one level to the following, whereas down arrows denote flows to detritus and curved arrows indicate respiration. All flows are expressed in $t.km^{-2}.year^{-1}$. P is the primary production and D is the detritus, both at TL 1.

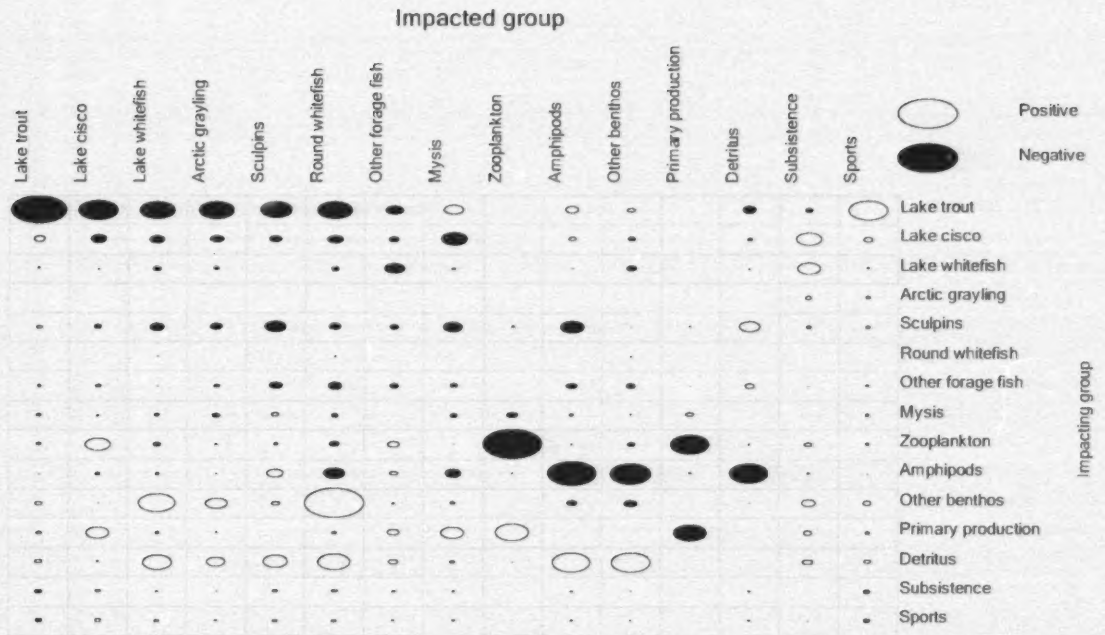


Figure 4. Mixed trophic impact analysis of Great Bear Lake ecosystem. White circles represent a positive impact and black circles indicate a negative impact; and the sizes of circles are proportionate to the degree of the impacts.

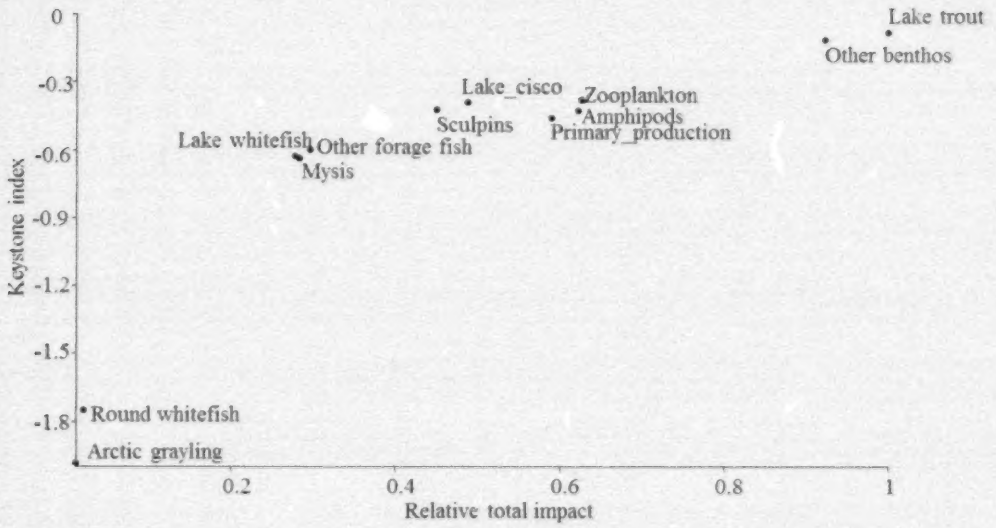


Figure 5. Keystoneness of different functional groups in Great Bear Lake. Keystone groups are those with a higher keystone index and relative total impact.